Climate-driven shifts in pelagic fish distributions in a rapidly changing Pacific Arctic

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Baseline surveys of offshore pelagic fishes in the eastern Chukchi Sea in 2012 and 2013 found that age-0 Arctic cod (*Boreogadus saida*) dominated the pelagic fish community in summer, with relatively few adults present in the region. Since this time, drastic changes in the ocean-atmosphere-ice feedback loop have led to continued warming, further reducing ice cover, and increased northward transport has led to an increase in Pacific-origin waters on the Chukchi shelf in summer. To examine potential bottom-up effects of these environmental changes on pelagic fishes in this rapidly changing environment, we extended a time series of large-scale acoustic-trawl surveys with additional surveys in 2017 and 2019. Age-0 Arctic cod were the most abundant pelagic fish in all four survey years, comprising 68-93% of fish abundance. However, age-0 walleye pollock (*Gadus chalcogrammus*), which were scarce (<0.1% of fishes) and confined to the southern Chukchi in 2012 and 2013, were present in high abundance (>21% of fish abundance) throughout the Chukchi shelf in 2017 and 2019. Age-0 Arctic cod were substantially more abundant in 2017 than in other years, possibly due to increased survivorship of larvae under warm conditions. Unlike in 2017, Arctic cod and pollock were spatially separated in 2019 due to enhanced transport, with Arctic cod primarily present in the northeastern portion of the survey area, which was characterized by cool surface and bottom temperatures. The substantial increase in abundance of age-0 pollock in recent years suggests that environmental conditions now allow this species to extend its northern range into the southern and central Chukchi Sea, at least on a seasonal basis. The changes in abundance and species composition...
of pelagic fishes in the 2012-2019 time series are tightly coupled to recent changes in
sea ice, temperature, and the increasing transport of Bering Sea waters through Bering
Strait into the Chukchi Sea. Given that the environment is expected to experience
further warming and increased transport, these northward shifts in species distribution
are likely to persist in the future.
1. Introduction

Arctic gadids, particularly Arctic cod (*Boreogadus saida*, also referred to as polar cod), have historically dominated the pelagic fish community in the Pacific Arctic ecosystem of the northern Bering, Chukchi, and Beaufort Seas (Alverson and Wilimovsky, 1966; Quast, 1974; Logerwell et al., 2015; De Robertis et al., 2017b). Arctic cod is a circumpolar-distributed species found throughout the Arctic Basin and surrounding marginal seas (Mecklenburg et al., 2018). Arctic cod are abundant lipid-rich (Copeman et al., 2017; Copeman et al., 2022a) prey that serve as an energy-dense trophic link between lower trophic levels and piscivores such as seabirds and marine mammals (Bradstreet et al., 1986; Matley et al., 2012). Trophic mass balance models of the Chukchi Sea indicate that Arctic cod are central to the food web and represent a substantial portion of seabird (>20%) and piscivorous mammal (>40%) diets (Whitehouse et al., 2014).

The Chukchi Sea is warming rapidly: mean summer/fall water column temperatures in the Chukchi Sea have increased by 0.1 °C decade\(^{-1}\) over the past century (Danielson et al., 2020). This warming is likely to accelerate. Air temperatures in the Arctic are anticipated to increase by >5 °C by 2100 (Overland et al., 2019). Climate predictions suggest that the duration of seasonal ice cover will continue to decrease at a rate of 0.94 days year\(^{-1}\) (Wang et al., 2018) as wind patterns change, and transport of water, including heat, into the region continues to increase.

The Chukchi is highly advective, with substantial transport of warm water from the Pacific entering through the Bering Strait in spring and summer (Woodgate et al.,
The associated northward heat flux helps to initiate the seasonal retreat of the Chukchi shelf sea ice (Woodgate et al., 2010). Transport through the Bering Strait has been increasing from its previous climatological average of ~0.8 Sv at a rate of ~0.01 Sv year\(^{-1}\) in recent decades (Woodgate, 2018). Shorter periods of ice cover (Baker et al., 2020b) further reduce the albedo of the sea surface in spring and summer, increasing solar warming which further accelerates ice melt in spring and delays ice formation in fall (Danielson et al., 2020). Over the past decade in particular, changes in this ice-ocean-atmosphere feedback loop have resulted in a substantial shift in the sea-ice extent and regional wind, with more extreme reductions in sea ice occurring since 2017 (Stabeno and Bell, 2019; Ballinger and Overland, 2022). The impacts of these continued environmental changes on pelagic fishes such as Arctic cod remain unclear.

The physiology and recruitment success of Arctic gadids is highly temperature-dependent and species-specific (Mueter et al., 2011; Laurel et al., 2016; Koenker et al., 2018). Changes in habitat suitability resulting from shifts in Bering Strait transport are particularly important for early life stages, for which survival is largely dependent on the ability to maximize growth and lipid stores prior to winter (Bouchard et al., 2017; Copeman et al., 2022b). Thus, changes in transport of heat, reduction in sea ice, and increased solar warming in the Chukchi are likely to affect the abundance of fishes and their role in energy transfer within Arctic food webs. Continued warming may affect the relative abundance and distributions of different species (Laurel et al., 2016; Baker, 2021). For example, boreal (subarctic) species such as walleye pollock (\textit{Gadus chalcogrammus}, hereafter pollock) and Pacific cod (\textit{Gadus macrocephalus}) may benefit
from warming (Marsh and Mueter, 2020), while Arctic species may be negatively
impacted by reduced habitat (Baker, 2021) and increased competition (Bouchard et al.,
2017).

Globally, boreal species have expanded their distributions northwards into the
Arctic as high-latitude regions have warmed (Wassman et al., 2011). The Barents Sea,
for example, is a shallow marginal sea of the Arctic Ocean which shares many
commonalities with the Chukchi Sea (Hunt et al., 2013). Rapid warming in the Barents
Sea has changed the spatial distribution of fish communities as subarctic species
expand northward on the shelf (Fossheim et al., 2015), further extending their
distributions into the Arctic Basin with the increased northward transport of warm
subarctic waters (Snoeijs-Leijonmalm et al., 2022). There is recent evidence of major
shifts in the distribution of adult fishes in the Bering Sea, where boreal species such as
pollock and Pacific cod have expanded their range northwards (Stevenson and Lauth,
2019; Eisner et al., 2020; Spies et al., 2020). Similarly, the southern limits of Arctic
species such as Arctic cod have shifted farther north, with boreal species taking their
place (Marsh and Mueter, 2020; Baker, 2021).

Northward advection from the Bering Sea structures the species composition of
pelagic communities in the Chukchi Sea. Transport from the south brings planktonic
organisms of Pacific-origin onto the Chukchi shelf (Eisner et al., 2013; Sigler et al.,
2017) and variability in northward flow can alter their rate of transport across the shelf
(Ashjian et al., 2021). Northward advection across the Chukchi shelf is also
hypothesized to structure the spatial distributions of age-0 fishes, as the average
current speeds surpass their sustained swimming abilities (Levine et al., 2021; Vestfals
et al., 2021). Age-0 gadids observed on the northern Chukchi shelf in summer are predicted to have been transported from spawning locations to the south in the northern Bering and southern Chukchi seas (Vestfals et al., 2021). Age 1+ gadids are scarce in pelagic habitats of the Chukchi Sea (De Robertis et al., 2017b), likely because as juveniles they are transported northward off the shelf by the prevailing currents (Levine et al., 2021; Vestfals et al., 2021). Arctic cod exhibit low genetic differentiation across the Pacific Arctic (Nelson et al., 2020), and northward transport may be driving the connectivity of the population across the Bering, Chukchi, and western Beaufort Seas. However, increased northward transport may reduce the residence time for growth in high productivity regions on the Chukchi shelf, with negative consequences for juvenile survival (Levine et al., 2021).

Surveys were conducted in 2012 and 2013 to establish a baseline of the distribution of pelagic fishes in the northern Bering and Chukchi seas (De Robertis et al., 2017b). Similar to previous observations in the region (Norcross et al., 2013; Logerwell et al., 2015), large numbers of Arctic cod were observed, with the greatest abundances in the northern Chukchi Sea. However, these were primarily age-0 fish with an average length of 3.5 cm, with <0.3% larger than 6.5 cm (De Robertis et al., 2017b). Given the relatively high abundances of age-0 fish at a critical life stage, the Chukchi shelf may serve as an important nursery area (De Robertis et al., 2017b; Levine et al., 2021). If so, continued warming of the Chukchi has the potential to negatively impact the growth and survival of this population. Given the dramatic recent changes in this environment (Ballinger and Overland, 2022), further investigations of environmental
factors influencing Arctic cod abundance and distribution are needed to better understand how changing climate may alter this ecosystem.

To examine longer-term trends in pelagic fishes in this rapidly changing environment, we extended the time series of pelagic fish surveys collected in 2012 and 2013 with additional surveys in 2017 and 2019. These surveys were designed to be comparable to the previous surveys, enabling us to assess the impacts of temperature and transport on the distribution of the abundant pelagic fish population in this highly dynamic region. The primary objectives of the study were to characterize the abundance and distribution of the major pelagic fishes in the Chukchi Sea, and to identify environmental drivers that influence the Chukchi Sea pelagic fish community.

Future changes in sea ice, temperature, and transport that result from a changing climate on the Chukchi shelf are likely to be drastic and the consequences for the age-0 Arctic cod population are unclear. Our goal was to better understand the mechanisms structuring the pelagic fish community in the Chukchi Sea to improve predictions of how future environmental changes will affect these populations.

### 2. Methods

Acoustic-trawl (AT) surveys were conducted in the U.S. continental shelf region of the Chukchi Sea and coastal regions of the western Beaufort Sea (Fig. 1) as part of the North Pacific Research Board Arctic Integrated Ecosystem Research Program (Baker et al., 2020a). As detailed in section 2.3 below, AT surveys use targeted trawls in
regions of high acoustic backscatter to ground-truth acoustic observations and convert
acoustic backscatter to estimates of fish abundance by species and size (Simmonds
and MacLennan, 2005), making it possible to efficiently survey large areas. The surveys
were conducted from 11-17 August and 28 August to 27 September 2017, and 27
August to 26 September 2019 on the R/V *Ocean Starr* (Figs. 1, A.1). Stations were
arranged on a 1° longitude and 0.5° latitude grid in 2017. Transect spacing was
increased to a 0.75° latitude grid in 2019. Sampling stations were occupied as the
vessel reached these locations along the transects. The survey began in the northern
Chukchi Sea and progressed south. The surveyed area was relatively shallow: bottom
depths were <60 m in 93% of the survey area in 2017 and 91% of the survey area in
2019. Acoustic data were collected as the ship transited at ~3.3 m s⁻¹ along survey
transects oriented in an east/west direction. To limit the potential bias caused by
changing vertical distribution of species throughout the day, only data collected during
daylight were included in the analysis. In addition to the planned transects, observations
collected during daylight while transiting between transects were also included in the
analysis.

Survey methods were consistent with previous work conducted in 2012 and 2013
(De Robertis et al., 2017b), as described below. The 2012 and 2013 surveys of the
Chukchi Sea both took place from 7 August to 8 September. This was approximately 3
weeks earlier than the surveys in 2017 and 2019. These earlier surveys sampled the
same area as in 2017 (Fig. 1a), occupying the same stations. However, in 2012 and
2013, the vessel transited from south to north. Due to the differences in survey
direction, the region south of 70.5 °N was sampled 15-40 days later in both 2017 and
2019 than 2012 and 2013, while transects north of 70.5 °N were sampled within the same 10–15-day period (Fig. A.1)

2.1. Acoustic data collection

Acoustic backscatter at 38 and 120 kHz was measured using a split-beam Simrad EK60 echosounder operating ES38B and ES120-7C transducers mounted at 3.7 m depth on the vessel’s hull. Data were collected using a pulse length of 0.5 ms at a ping rate of 2 Hz. In deep water (>250 m), longer pulse lengths (1 ms at 120 kHz, 4 ms at 38 kHz) were used to increase signal-to-noise ratios, and the ping rate was slowed to ~0.3-0.5 Hz. The echosounders were calibrated twice each survey at the shorter pulse length and once each survey at the longer pulse length using the standard sphere technique (Demer et al., 2015). Results from the two 0.5 ms pulse length calibrations in each year were averaged before being applied in post-processing. Calibration results were consistent among surveys. Gains from the averaged pre- and post-survey calibrations for the 0.5 ms pulse length differed by 0.09 dB (2.2%) at 38 kHz and 0.17 dB (4.0%) at 120 kHz. Mean sound speed and absorption coefficients for each year were calculated from conductivity, temperature, and depth (CTD, Sea-Bird Electronics 911plus) sensor profiles conducted at survey stations (Fig. 1, 39 profiles in 2017 and 46 profiles in 2019) and applied in post-processing.

2.2. Midwater trawl sampling
The species and size composition of pelagic acoustic scatterers were determined from targeted midwater trawls in areas of high backscatter. Acoustically observed fish aggregations were sampled using a modified Marinovich herring trawl equipped with the same fine-mesh 2 by 3 mm codend liner used in previous surveys (De Robertis et al., 2017b). Backscatter was generally evenly distributed throughout the survey area. Thus, many trawl hauls were conducted at the survey sampling stations (Fig. 1) for logistical convenience. The hauls targeted the depth of greatest backscatter at each location.

Prior to the 2017 survey, the Marinovich trawl was modified with a redesigned aft section that resulted in lower selectivity and better retention of small fishes (De Robertis et al., 2022). Midwater trawls were conducted at 33 sites in 2017 and 43 sites in 2019 (Fig. 1), with an average ship speed of 1-1.5 m s⁻¹ during trawling. Net openings and depths were monitored with either a Simrad FS70 or Marport Trawl Explorer net sounder attached to the headrope. The trawl opening was approximately 8 m horizontal by 7.5 m vertical, with a mean headrope depth of 27.1 m (range 11.4-46.7 m) in 2017 and 34.9 m (range 13.2-227.9 m) in 2019.

Trawl catches were weighed, sorted, and identified to species. Fish lengths (3392 individuals in 2017, 9124 in 2019) and jellyfish bell diameters (1211 individuals in 2017, 751 in 2019) were measured on a subsample of individuals from each trawl (up to 60 gadids, 10 of all other species) to the nearest 1.0 mm using an electronic measuring board (Towler and Williams, 2010). The protocols for length measurement varied among years for the key gadid species. Age-0 gadid length was measured as total length in 2017 and standard length in 2019. To account for these differences, we
conducted repeat measurements of fork, total and standard length on the same individuals and calculated linear models to convert among length types (Table A.1). Genetic analyses indicated that the field identifications of juvenile gadids were unreliable, particularly when distinguishing between age-0 Arctic cod and pollock (Wildes et al., 2022). Thus, genetic markers extracted from tissue samples from a subsample of measured gadid fishes (894 in 2017, 3155 in 2019) were used to confirm field identifications. For gadids with a tissue sample (40% and 56% of measured gadids in 2017 and 2019, respectively), the species identifications were updated based on the genetic identifications (see Wildes et al., 2022 for details). For the remaining measured gadids with no genetic identification, species was assigned probabilistically based on the length-dependent species composition of the genetically identified individuals in that haul (see Appendix B).

2.3. Data processing and abundance estimation

Fish abundances were estimated by combining backscatter measurements and size and species composition information from the genetically corrected trawl samples following the methods in De Robertis et al. (2017b). The 38 kHz acoustic backscatter was integrated in 0.5 nmi along-transect intervals with a minimum $S_v$ threshold of -70 dB re 1 m$^{-1}$, excluding data shallower than 6.5 m (due to the draft of the ship) and deeper than 0.5 m above the seafloor. Trawl catches were corrected for size- and species-dependent net selectivity based on small-mesh recapture nets mounted to the trawl to account for the size- and species-specific likelihood of capture (De Robertis et al.,
Pacific cod were too scarce to estimate net selectivity for the species, so
the selectivity relationship for pollock was applied as the fish are of similar origin and
morphology. There were no estimates of selectivity for invertebrates so values for these
species were not corrected for selectivity; however, these species are very weak
contributors to scattering relative to fish with swimbladders, and the lack of selectivity
corrections for these taxa is unlikely to affect the abundance estimates of other species
(De Robertis et al., 2017b).

The selectivity-corrected size and species composition estimates were combined
with size- and species-specific scattering properties to allocate observed acoustic
backscatter to each species in the catch. Target strength relationships from the
literature were used to estimate acoustic scattering for each species in the trawl catch
(see De Robertis et al., 2017b, their Table 1). The proportion of total areal backscatter
attributable to each species was then calculated along acoustic transects using species
and size compositions from the nearest trawl (De Robertis et al., 2017b, their equations
1-7). The AT method is best-suited for abundant, strongly-scattering species
(Simmonds and MacLennan, 2005). The analysis was thus limited to Arctic cod, pollock,
Pacific cod, saffron cod (*Eleginus gracilis*), Pacific herring (*Clupea pallasii*), and capelin
(*Mallotus catervarius*). These species accounted for 96.2% and 63.7% of fish by
number in the trawl catch in 2017 and 2019, respectively. The contribution of other less
abundant or weakly scattering species to the observed backscatter was estimated, but
abundance estimates are not reported. For example, as in previous surveys, we were
unable to estimate Arctic sand lance (*Ammodytes hexapterus*) abundance using AT
methods with confidence. This is because they are weak acoustic scatterers due to their
lack of a swimbladder, which results in high uncertainty if stronger scatters are misclassified as sand lance (Yasuma et al., 2009; De Robertis et al., 2017b).

2.4. Environmental data collection and processing

At all stations, a CTD sensor was deployed from surface to ~5 m above the seafloor. Mean water column temperature and salinity was calculated at each station for the upper 10 m (hereafter referred to as surface temperature/salinity), and the deepest 5 m (hereafter referred to as bottom temperature/salinity) of each profile. Measurements were available from 39 stations in 2017 and 46 stations in 2019. To associate fish with environmental conditions, each 0.5 nmi interval of transect was assigned to the nearest CTD station, and the average fish abundances (fish m⁻²) for each grouping of intervals were calculated. Water mass classifications from Danielson et al. (2017) were used to describe station conditions based on temperature: 2 °C and 7 °C were used to represent the boundaries between Alaskan Coastal Water (>7 °C), Bering/Chukchi Summer Water (2-7 °C), and Bering Chukchi Winter Water (<2 °C).

2.5. Availability of 2012 and 2013 data

Acoustic estimates of abundance from surveys conducted in 2012 and 2013 for Arctic cod, pollock, Pacific cod, saffron cod, Pacific herring, and capelin (De Robertis et al., 2021) were included in our analyses to provide context for the new observations in 2017 and 2019. Depth-stratified data from these surveys were not available; thus, only
spatial comparisons were conducted across the four years of abundance estimates. Surface and bottom temperature and salinity as calculated for 2017 and 2019 were available from the 2012 (68 CTD profiles) and 2013 (55 CTD profiles) surveys (Danielson et al., 2017). A subsample of gadids collected in 2012 and 2013 (De Robertis et al., 2017b) were validated using the same genetic marker analyses used for gadids collected during the 2017 and 2019 surveys. This analysis indicated that, in contrast to the more recent surveys, few pollock were present in the survey region (0.2% of 1,435 gadids analyzed from both years, Wildes et al., 2022). This provided confidence for further comparison of the 2017/2019 surveys with the 2012/2013 data, despite the potential for species misclassifications due to the lack of genetic-based species assignments in the 2012/2013 surveys.

3. Results

3.1. Results of the 2017 and 2019 surveys

3.1.1. Trawl catches

Catch rates were >6-fold higher in 2017 than in 2019 (mean catch per unit effort for all fishes of 0.248 fish m\(^{-3}\) in 2017 and 0.034 fish m\(^{-3}\) in 2019) primarily due to high abundances of Arctic cod (0.189 fish m\(^{-3}\) in 2017 and 0.017 fish m\(^{-3}\) in 2019). Trawl catches were dominated by small fishes (80% <7.3 cm in 2017 and <8.0 cm in 2019). Juvenile gadids (Arctic cod, pollock, saffron cod, Pacific cod), Arctic sand lance,
pricklebacks (*Stichaedae*), Pacific herring, and capelin accounted for 98.6% of catch by number (16.0% by weight) in 2017, and 93.4% of catch by number (6.7% by weight) in 2019 (Fig. 2a, b). These species accounted for 95.2% and 87.3% of the catch by number in 2012 and 2013, respectively (De Robertis et al., 2017b). Jellyfish composed a small proportion of the catch by number (0.7% in 2017, 5.5% in 2019), but a large proportion of the catch by weight (83.8% of the biomass in 2017, 93.1% in 2019). *Chrysaora melanaster* were prevalent throughout the survey area in both years, accounting for 60.8% of all jellyfish by weight in 2017 and 58.3% in 2019. Catch compositions of nearby trawls were relatively consistent (Fig. 2a, b), justifying the extrapolation of catch composition from nearest hauls to the fine-scale acoustic observations.

Age-0 Arctic cod dominated the catch throughout the survey region in 2017, except in the southern Chukchi (south of 68.5 °N) where the catch composition was highly variable (Fig. 2a). Age-0 pollock were widely distributed and captured at lower abundance than Arctic cod throughout the survey area (Fig. 2a). The catch composition was more spatially stratified in 2019, with Arctic cod primarily restricted to the northeastern part of the survey area (Fig. 2b). The northwestern part of the survey area was dominated by pollock and Arctic sand lance. South of 71 °N, pollock were the most abundant fishes in the trawl catches, with capelin and Pacific herring occurring at some nearshore locations (Fig. 2b).

3.1.2. Acoustic backscatter
Mean backscatter in 2017 was 4.5-fold higher than in 2019 (Table 1). Acoustic backscatter in 2017 was high throughout the survey region north of 68 °N, coinciding with the areas where age-0 Arctic cod were numerically abundant in trawl catches (Fig. 2c). The greatest acoustic backscatter in 2019 occurred between 70 and 72 °N, where age-0 Arctic cod and pollock dominated the catch (Fig. 2b, d). Patchy high-backscatter schools in the southern Chukchi Sea in 2019 were attributed to Pacific herring (Figs. 2d, A.3).

Age-0 gadids (i.e. Arctic cod, pollock, saffron cod, and Pacific cod) were the primary contributors to 38 kHz backscatter. Together, they accounted for 94.3% of the backscatter in 2017 and 88.3% in 2019. Capelin and Pacific herring were the next most abundant sound scattering pelagic species, accounting for 1.9% of the backscatter in 2017 and 5.5% in 2019. Although jellyfish dominated the biomass, they have a much lower mass-specific target strength than fishes with swimbladders (De Robertis and Taylor, 2014) and were not major contributors to the observed backscatter (<1.3% in both years).

3.2. Acoustic estimates of fish abundance and distribution

3.2.1. Abundance, distribution, and body size of Arctic gadids

Juvenile gadids dominated the acoustic-trawl abundance estimates in 2017 and 2019. They composed 98% of fishes in 2017 and 96% in 2019. Arctic cod were most abundant, comprising 76.3% of fish abundance in 2017 and 68.6% in 2019. Arctic cod also dominated AT abundance estimates in the previous 2012 and 2013, comprising
>93% of fishes in both years. High abundances of small pollock were observed in 2017 and 2019. Pollock made up 21.1% of fishes in 2017 and 26.6% in 2019. This was substantially higher than the abundance of pollock in the earlier surveys, in which they were essentially absent; pollock accounted for only 0.1% of fishes in 2012 and <0.001% of fishes in 2013 in trawl catches north of 66 °N. Other species (Saffron cod, Pacific cod, capelin, and Pacific herring) were present at much lower abundances in 2017 and 2019 (Table 1, Fig. A.3). Abundances of Arctic cod and pollock in 2017 were 5.7- and 4.0-fold greater than in 2019, respectively (Table 1). Arctic cod and pollock densities in 2017 were greater in the central and northern Chukchi compared to other survey years (Fig. 3). Furthermore, the relatively high densities of Arctic cod in 2017 were widespread and extended throughout much of the shelf. Pollock were also distributed throughout the survey region at much greater densities than previously observed (Fig. 3e, f).

The lengths of Arctic cod and pollock were consistent with age-0 fishes for these species (Fig. 4, Brodeur et al., 2002; Helser et al., 2017). This classification for Arctic cod was confirmed by otolith aging of a subsample (n=77) of fish captured in the 2017 survey (Chapman et al., 2022). Arctic cod length averaged 4.4 ± 0.5 cm (SD) in 2017, and 4.7 ± 0.5 cm in 2019 (Fig. 4a). The Arctic cod in 2017 and 2019 were on average ~1 cm larger than those observed north of the Bering Strait in 2012 and 2013 (mean length was 3.5 cm in both years, Fig. 4a). Fishes sampled on the same date were larger in the 2017 and 2019 surveys, suggesting they experienced higher growth rates than in 2012 and 2013 (Fig. A.2). Pollock mean length was 4.9 ± 0.6 cm in 2017 and 5.2 ± 0.4 cm in 2019 (Fig. 4b). The mean length of the few pollock present in 2012 and 2013 was 4.9 ± 0.5 cm and 6.8 ± 0.7 cm, respectively.
3.2.2. Environmental conditions and associations

Arctic cod and pollock exhibited associations with temperature and salinity but these were not consistent among surveys (Fig. 5). Surface temperature and salinity at sampling stations ranged from 2.5 to 7.5 °C and 25.4 to 32.3 in 2017 (Fig. 5e), and 3.2 to 10.6 °C and 27.1 to 32.1 in 2019 (Fig. 5g). Relative to other years, surface temperatures in 2017 fell within a relatively narrow band of intermediate temperatures. Bottom temperature and salinity ranged from -0.7 to 6.5 °C and 31.0 to 34.7 in 2017 (Fig. 5f), and -1.4 to 10.6 °C and 29.1 to 34.7 in 2019 (Fig. 5h). In both years, the coldest surface and bottom waters were encountered in the northeastern portion of the survey area (Fig. A.4).

In 2017, Arctic cod and pollock distributions overlapped broadly and both species inhabited similar water masses (Figs. 3c, g, 5e, f). In contrast, in 2019, the two species were spatially separated and experienced different thermal environments (Figs. 3d, h, 5g, h). Pollock were the primary gadids in the southern and western portion of the survey area in 2019 (Fig. 3h), which exhibited warm (>7 °C) surface temperatures that typify Alaskan Coastal Water and warm (>2 °C) bottom waters typical of Bering/Chukchi Summer Water (Figs. 5g, h, A.4). Conversely, Arctic cod were largely restricted to the northeastern region of the survey area in 2019 (Fig. 3d), where surface temperatures were <7 °C (Figs. 5g, A.4d) and bottom temperatures were <2 °C, typical of Bering/Chukchi Winter Water (Figs. 5h, A.4h).

Arctic cod and pollock were distributed closer to the surface in regions with cold bottom water (Fig. 6). Fishes were relatively evenly distributed throughout the water
column in 2017 (Fig. 6a, b) when water across the shelf was less thermally stratified (Figs. 5e, f, A.4c, g), and >65% of the total survey abundance was in areas with bottom water >2 °C. Only 25% of pollock and Arctic cod were in areas with bottom water >2 °C in 2019; fishes in these locations were more evenly distributed throughout the water column (Fig. 6c, d), with only 28% of the abundance shallower than 25 m. Arctic cod were largely restricted to areas with bottom waters <2 °C in 2019 (Figs. 5h, 6c), which was not the case in previous years (Fig. 5b, d, f). In the colder regions of the survey area (bottom temperature <2 °C), >55% of the fishes were shallower than 25 m in 2019, driven by the relatively large abundance of Arctic cod (and to a lesser extent, pollock) high in the water column (Fig. 6c, d).

4 Discussion

4.1. Abundance and distribution of fishes

Observations from four surveys spanning a seven-year period suggest that the pelagic fish community in the Chukchi Sea is continuing to undergo rapid change associated with the accelerated warming observed over the past decade. While age-0 gadids continue to dominate the pelagic fishes on the Chukchi shelf (Logerwell et al., 2015; De Robertis et al., 2017b), their abundance and species composition were highly variable. Age-0 gadids were substantially more abundant in 2017 relative to the other years, which was apparent in both the acoustic-trawl (AT) abundance estimates and the
trawl catch. This was due to both a large increase in Arctic cod and an influx of pollock.

While age-0 Arctic cod continue to be the dominant pelagic fish in much of the eastern Chukchi Sea, age-0 pollock, which were previously near-absent in the region, were present in substantial numbers in 2017 and 2019.

Arctic cod, pollock, saffron cod, Pacific cod, and capelin were the most abundant species in 2017 and 2019. Pacific herring were also present in the southern portion of the survey area within Kotzebue Sound in 2019 (Table 1, Fig. A.3). With the exception of pollock, these same species were dominant in the 2012 and 2013 AT survey observations (De Robertis et al., 2017b) and in other recent surveys of the Pacific Arctic (Eisner et al., 2013; Goddard et al., 2014; Logerwell et al., 2015). Although we were unable to confidently estimate the abundance of Arctic sand lance using AT methods due to their weak acoustic scattering, they were abundant in trawl catches in the central and northwestern portion of the survey region in 2019 (Fig. 2b; also see Baker et al., 2022).

4.2. Relative abundances of age-0 and age-1+ gadids

In comparison to the high densities of age-0 gadids present in the survey area, relatively few age-1+ gadids or other large fishes were observed. This is consistent with other surveys of both the pelagic (De Robertis et al., 2017b) and demersal (Goddard et al., 2014; Logerwell et al., 2015) communities in the eastern Chukchi Sea conducted over the past decade. Although fish captured in bottom trawls tend to be larger (Barber et al., 1997; Goddard et al., 2014; Maznikova et al., 2022), their densities are
substantially lower than the age-0 fishes observed in recent pelagic surveys (see
discussion in De Robertis et al., 2017b). Historically, sampling in shallow (<20 m)
nearshore regions of the Chukchi Sea suggests that densities of larger Arctic cod may
be higher in those environments (Alverson and Wilimovsky, 1966; Thedinga et al.,
2013). There are also large colonies of piscivorous seabirds associated with these
areas, indicating that larger fishes are likely present (Swartz, 1966; Piatt et al., 1991).
However, in contrast with these observations as well as surveys of the western Beaufort
Sea (Craig et al., 1982; Frost and Lowry, 1983; Parker-Stetter et al., 2011), we did not
observe many large Arctic cod in the pelagic environment of the Chukchi Sea surveyed
in this study.

Bottom trawls indicate that while relatively low in density (~0.01 fish m$^{-2}$), age 1+
Arctic cod are present throughout the western Chukchi Sea (Maznikova et al., 2022).
Surveys of the Russian sector of the Chukchi shelf in 2018 found primarily age-1 to age-
3 Arctic cod in the southern portion of the shelf, associated with the inflow of Pacific
water through Bering Strait (Maznikova et al., 2022). Farther north, age-0 and age-1+
Arctic cod have been observed along the shelf slope in the western Chukchi (Maznikova
et al., 2022). Juveniles were associated with the drifting sea ice and older individuals
were found deeper in the water column, associated with warm Atlantic water. Similar
aggregations at depth of age-1+ Arctic cod have also been observed along the shelf
slope in the eastern Chukchi (De Robertis et al., 2017b) and the Beaufort Sea (Geoffroy
et al., 2016). It is hypothesized that these aggregations of larger fish at depth may form
as juveniles move deeper in the water column following northward transport off of the
shelf (Levine et al., 2021; Maznikova et al., 2022).
Demersal sampling conducted concurrently with the 2017 and 2019 surveys of the eastern Chukchi sea further support the observations that compared to age-0 fish in the midwater, age-1+ Arctic cod are relatively scarce in the region during the survey period. A 3-m plumb-staff beam trawl (Gunderson and Ellis, 1986) was used to sample demersal fishes and benthic fauna at survey sampling stations (66 trawls in 2017, 52 trawls in 2019) (Logerwell and Cooper, 2021a; Logerwell and Cooper, 2021b). While this net is small, the selectivity for the size distribution of age-1+ Arctic cod observed in the western Chukchi shelf (Maznikova et al., 2022) is comparable to that of a larger trawl typically used for groundfish bottom trawl surveys (Kotwicki et al., 2017).

Estimated total abundances of age-1+ Arctic cod in the survey area were $1.0 \times 10^9$ (0.007 fish m$^{-2}$) in 2017 and $5.1 \times 10^8$ (0.003 fish m$^{-2}$) in 2019 (Logerwell and Cooper, 2021a; Logerwell and Cooper, 2021a). These densities are consistent with previous bottom trawl sampling in the eastern Chukchi Sea in which catches were primarily age-1+ Arctic cod occurring at relatively low densities (0.01 Arctic cod m$^{-2}$, Goddard et al., 2014; 0.001 to 0.08, Thedinga et al., 2013; 0.04, Norcross et al., 2013; 0.006 to 0.02, Barber et al., 1997). Compared to the age-0 population observed in the midwater in the survey area (this study; De Robertis et al., 2017b), these relatively low densities of age-1+ Arctic cod would represent age-0 survival of <1% if the eastern Chukchi Sea was a closed system. In a comparable environment such as the Barents Sea, age-0 Arctic cod survival is estimated to be approximately 10% (Marsh et al., 2019). Thus, consistent with the previous surveys, the relatively small age-1+ population present in the survey area in summer is likely the result of emigration of juveniles to other areas (De Robertis et al., 2017b; Marsh et al., 2019). Further, it is highly unlikely that the relatively low
abundance of mature Arctic cod present in the area in summer have the reproductive potential to produce the population of age-0 Arctic cod observed in the acoustic-trawl survey (Marsh et al., 2019).

We believe the scarcity of age-1+ gadids observed in the 2017 and 2019 surveys accurately represent the pelagic community composition in the area surveyed, as they have been corrected for gear selectivity (De Robertis et al., 2022). The gadid lengths from both surveys are consistent with acoustic observations made with an uncrewed surface vehicle in 2018, which inferred that pelagic fishes were primarily age-0 gadids based on the strength of echoes from individuals (target strength) and found little evidence of targets consistent with adult-sized gadids (Levine et al., 2021). In addition, no large gadids were caught in surface trawls using a large Nordic rope trawl (184 m long, ~315 m² net opening) as part of a separate study conducted during the 2017 and 2019 surveys (Farley and Levine, 2021a; Farley and Levine, 2021b). The absence of large gadids in the midwater in 2017 and 2019 cannot be attributed to the sampling gear, as the Marinovich herring trawl used in this study has retained larger individuals when used in other regions. For example, pollock up to 61 cm were captured in several Marinovich herring trawl hauls in the Bering Sea (Honkalehto and McCarthy, 2015). A bottom trawl (3 m vertical and 12 m horizontal trawl opening) similar in size to the Marinovich has also been effective at capturing adult pollock when fished in midwater (Kotwicki et al., 2017). Thus, we are confident that our trawl sampling establishes that relatively few pelagic adult gadids were present in the midwater within the survey area.

There is little evidence to support the presence of age-1+ Arctic cod in the near-surface region of the water column and above the sampling depth of the acoustic
observations. No large gadids were caught in surface trawls using a large Nordic rope trawl (184 m long, ~315 m² net opening) as part of a separate study conducted during the 2017 and 2019 surveys (Farley and Levine, 2021a, 2021b). While adult Arctic cod may also be associated with sea ice (Ponomorenko, 2000; David et al., 2016), our sampling was limited to ice free areas and little to no sea ice was present in the area during the period of the surveys in 2017 or 2019. It is possible that an age-1+ population is seasonally present in the eastern Chukchi Sea when sea ice is present. However, if these fish remain associated with sea ice into the summer, they likely migrate north, following the ice edge into the Beaufort and Arctic basin and were no longer present on the eastern Chukchi shelf by the time of the late summer surveys.

4.3. Recent colonization of the Chukchi Sea by pollock

The dramatic increase in age-0 pollock in the eastern Chukchi Sea is a recent occurrence. Small pollock and Arctic cod are difficult to distinguish based on external morphological characteristics in the field (Mecklenburg et al., 2018). Without genetic analyses, we would have almost completely failed to identify the unexpected presence of pollock within the survey area in 2017 (Wildes et al., 2022). Post-survey genetic identification was necessary to accurately estimate abundances and distributions of each species (see Appendix B for details). Although the spatial coverage of tissue samples from previous surveys is more limited, the available genetic analyses suggest that pollock were scarce in the survey region in 2012 and 2013 (Wildes et al., 2022).
Similar recent increases in pollock abundance have been reported in the western Chukchi Sea, where both age-0 and larger mature pollock have become substantially more abundant in the past decade. Though densities remain low (<0.005 fish m$^{-2}$), the total abundance of pollock observed in bottom trawl surveys of the western Chukchi Sea in 2018-2020 indicate a substantial increase relative to surveys prior to the recent period of intense warming that has occurred since 2017 (Emelin, et al., 2022; Maznikova et al., 2023). It is hypothesized that this population is primarily composed of migrants from the northern Bering Sea (Maznikova et al., 2023), and abundances in summer have become large enough in recent years to support commercial fishing in the region.

4.4. Increased body size of Arctic cod

Arctic cod were 25-35% (~1 cm) larger in 2017 and 2019 than in 2012 and 2013. Although the timing of surveys in 2017 and 2019 was later than in the previous surveys, the increase in body size is too large to be attributed to survey timing alone. The summer is a period of rapid growth for age-0 gadids on the Chukchi shelf (Levine et al., 2021; Deary et al., 2021), and the more recent surveys in 2017 and 2019 occurred approximately 3 weeks later than those in 2012 and 2013. For a 3.5 cm Arctic cod at 9°C, the temperature of maximum growth (Laurel et al., 2017), an additional 21 days (reflecting the timing of later surveys in 2017 and 2019) could explain approximately 0.5 cm of additional growth (based on Laurel et al., 2017, their Table 2 model B$_0$). However,
even at this maximum growth rate, this would only account for approximately half of the
increased size observed in 2017 and 2019.

Warmer water temperatures are likely to have contributed to the recent increases
in Arctic cod body size. Mean water temperatures between the approximate timing of
Arctic cod spawning and the survey dates (January to August, Fig. 7; Bouchard and
Fortier 2011) in the Bering Strait (A3 mooring site, 66.29 °N, 168.96 °W, Woodgate,
2018; Woodgate and Peralta-Ferriz, 2021) in 2017 and 2019 were 0.5-1.5 °C warmer
than in 2012 and 2013. This was driven principally by warmer conditions in spring and
summer (Fig. A.5). Exceptionally warm temperatures in spring 2017 were observed in
the Bering Strait (Fig. A.5a), when water was 0.5 °C warmer than the same period in
2019 and >1 °C warmer than in 2012 and 2013 (Fig. 7). Increased growth rates
resulting from warmer temperatures may have led to larger individuals in 2017 and 2019
(Laurel et al., 2017). Based on the growth rates of age-0 Arctic cod laboratory
specimens reported in Laurel et al., (2017), the ~1 °C difference in temperature
between the spawning period and survey (Fig. 7) could account for a ~0.5 cm increase
in length by the time of the survey in September (Fig. A.2).

Vertical habitat selection may have helped to maintain higher growth rates in
regions of cold bottom water. In 2017, both Arctic cod and walleye pollock were
relatively evenly distributed throughout the water column (Fig. 6a, b) when temperature
contrast between surface and bottom waters throughout the survey area was fairly low
(Fig A.4c, g). In 2019, when temperature contrast between the surface and bottom
waters was higher (Fig A.4d, h), distributions of both species tended to be shallower in
areas of cold bottom temperatures (Fig. 6c, d). This change in vertical distribution may
reflect a behavioral choice. That is, both species may be avoiding colder deep waters where growth potential is reduced (Laurel et al., 2016).

Increased survival of early-hatched Arctic cod larvae may have also contributed to increased mean size in 2017 and 2019. Observations of Arctic cod in the Canadian Arctic suggest that higher temperatures reduce time-to-hatch and improve the survival of early hatching larvae (Bouchard and Fortier 2011; Bouchard et al., 2017). Dupont et al. (2020) proposed that increased early-season survival rates would lead to older and larger age-0 Arctic cod. As length is strongly associated with hatch date (Bouchard et al., 2017), a greater proportion of older individuals leads to an increase in the mean length in the population. Improved early larval survival may also lead to increased size and lower mortality of age-0 fishes (Dupont et al., 2020), which may have contributed to the high abundances of age-0 Arctic cod observed in 2017. However, this increase in hatch survival does not necessarily equate with increased recruitment. Copeman et al. (2022a) found that Arctic cod in 2017 had significantly lower total lipids than in 2013, suggesting that though hatch success may increase as a result of warming, overwintering success may be reduced.

4.5. Impact of temperature on sources of age-0 gadids in the eastern Chukchi Sea

Although we do not know the source of the age-0 Arctic cod population observed on the Chukchi shelf, modeling studies predict that the population likely originates in the northern Bering Sea and/or southern Chukchi Sea, and is subsequently advected north (Levine et al., 2021; Vestfals et al., 2021). Arctic cod are known to spawn under sea ice
(Ponomorenko, 2000), and a migration path between spawning and feeding grounds has been proposed (Forster et al., 2020) where Arctic cod spawn near the ice edge in the northern Bering and Southern Chukchi Seas, follow the ice retreat north to seasonal feeding areas, and return to the spawning grounds in late fall. This migration may be altered by continued warming: the reduction in suitable habitat (bottom temperatures <2 °C) has led to decreases in Arctic cod in the northern Bering Sea in summer (Baker, 2021), indicating that spawning may be shifting farther north onto the Chukchi shelf.

The high abundances of age-0 pollock in the Chukchi Sea in recent years may be indirectly driven by increased temperatures in the northern Bering Sea associated with decreased ice extent and earlier ice retreat (Danielson et al., 2020). Few pollock of any age class have been observed north of the Bering Strait in previous surveys (Quast, 1974; Norcross et al., 2013; Lencerwell et al., 2015; De Robertis et al., 2017b; Maznikova et al., 2023). Ice cover in the Bering Sea has historically supported the formation on the eastern Bering Sea shelf of an extensive “cold pool” – a region where cold (<2 °C) bottom waters persist in summer and early fall (Wyllie-Echeverria and Wooster, 1998; Stabeno and Bell, 2019). Adult pollock typically avoid the cold pool and move to the outer shelf of the Bering Sea when the area of the cold pool is extensive (Kotwicki et al., 2005; Stevenson and Lauth, 2019). Reduced ice formation and shorter periods of ice cover lead to a diminished cold pool, which likely reduces the thermal barrier and enables adult pollock to remain on the inner and northern shelf throughout the year.

The Bering Sea has experienced extreme warming in recent years, which drastically reduced the size of the cold pool in both 2017 and 2019 (Stabeno and Bell,
Pollock distributions shifted northward during this period, resulting in high densities of adult pollock in the northern Bering Sea (Stevenson and Lauth, 2019; Eisner et al., 2020). Similarly, high abundances of juvenile and adult pollock were also observed in the Russian sector of the southern Chukchi Sea since 2018 (Maznikova et al., 2023). The increased abundance of juvenile and larger mature pollock on the western shelf is attributed to passive drift and active migration from the northern Bering Sea, respectively (Emelin et al., 2022). Across the shelf, pollock were likely absent in 2012 and 2013 due to the presence of an extensive cold pool (O'Leary et al., 2020). Thus, the recent northward shift of pollock distribution combined with the prevailing northward transport has likely increased the supply of larval pollock to the Chukchi shelf.

4.6. What led to the spatial separation of gadids in 2019?

Given that Arctic cod and pollock were associated with distinct water masses in 2019, we hypothesize that the spatial separation between these species was driven by differences in spawning locations. Pollock were abundant in the central and southern portions of the survey area in 2019, where surface temperatures exceeded 8 °C (Figs. 3, 5). These temperatures indicate that pollock were largely present in Alaskan Coastal Water, which primarily originates on the inner Bering Sea shelf, driven by river input in spring and summer (Coachman et al., 1975; Woodgate et al., 2005). In 2012 and 2013, this water was restricted to nearshore regions of the eastern Chukchi. However, in 2019, Alaskan Coastal Water was found as far north as 72 °N and extended well
offshore (Fig. A.4), likely due to southward winds forcing the current away from the coast (Woodgate et al., 2015; Morris, 2019). Age-0 pollock were likely advected within this Bering Sea-origin water mass, potentially explaining their widespread distribution in the Chukchi Sea.

The spatial separation in 2019 may reflect a northward shift in the spawning locations of Arctic cod as a result of further warming. Arctic cod and pollock overlapped broadly in 2017 (Fig. 3c, g), with both species co-occurring in the relatively narrow range of intermediate surface and bottom temperatures found in the survey area compared to other years (Fig. 5e, f). This suggests that spawning locations of Arctic cod may have overlapped with those of pollock in the northern Bering Sea where a reduced cold pool led to suitable conditions for both species (Baker, 2021). We hypothesize that Arctic cod were spawned farther north in 2019 than in 2017 due to the extreme low ice conditions (Stabeno and Bell, 2019). In 2019, Arctic cod were present largely in areas of cold (<2 °C) bottom waters (Fig. 5h) characteristic of Winter Water (Lowry et al., 2015; Woodgate, 2018; Danielson et al., 2020). This water mass would have been present over the Chukchi shelf prior to the input of warm Alaskan Coastal Water in spring, indicating that Arctic cod may have been spawned on the Chukchi shelf. However, the pollock spawning location may have been consistent with 2017, as they were once again present in areas characteristic of the Bering Sea-origin Alaska Coastal Water.

Bering Strait transport between the approximate time of first spawning of Arctic cod and the survey (January to August) was substantially higher in 2019 relative to previous years (Fig. 7). Given that survey timing was similar in 2017 and 2019 (Fig. A.1), this increased transport likely led to a northward shift in the distributions of both
species, and possibly led to the advection of a portion of the age-0 Arctic cod population off the Chukchi shelf by the time of the survey. A similar effect of transport has been observed in zooplankton: in years of weak westward winds, the dominant northward transport of water across the Chukchi shelf results in an increase in the presence of Bering Sea origin zooplankton in August near Pt. Barrow (Ashjian et al., 2021). This is consistent with the displacement of fishes to the north as observed in 2019 when transport was high (Fig. 7). Conversely, strong westward and southward winds inhibit northward transport on the shelf, resulting in retention of plankton and small fishes (Ashjian et al., 2021; Levine et al., 2021).

4.7. The future of pelagic fishes on the Chukchi shelf

We propose that the observations of gadids in this short survey time series can be described by a conceptual model encompassing three environmental regimes. Under the conditions of the last decade (i.e. 2012/2013 or “recent conditions”, Fig. 8a), ice in the northern Bering Sea retreats in May and June (Frey et al., 2015), the Chukchi Sea remains relatively cool and surface waters reflect a mixture of melt water, Bering/Chukchi Summer Water, and Alaskan Coastal Water (Danielson et al., 2017). In this regime, age-0 Arctic cod, which are likely to have been spawned as far south as the northern Bering Sea (Vestfals et al., 2021), are the dominant gadids on the Chukchi shelf in late summer. In late summer, they are primarily present in the northeastern Chukchi Sea, where they experience intermediate temperatures as Winter Water
warms. These fish are then advected northwards during the fall towards the Chukchi and Beaufort shelf breaks and into the Arctic Ocean (Levine et al., 2021).

Under warming ocean conditions such as those observed in 2017, when ice retreats from the northern Bering Sea earlier in spring (Wang et al., 2018), we propose a “warming” regime (Fig. 8b). Temperatures are warmer across the shelf as a result of decreased sea-ice extent and earlier ice retreat. With a reduced cold pool in the Bering Sea, the density of spawning adult pollock near the Bering Strait increases. This leads to an increased supply of age-0 pollock in the northern Bering Sea, which are advected onto the Chukchi shelf (Eisner et al., 2020; Baker, 2021; Emelin et al., 2022; Maznikova et al., 2023). Hatch success of gadids also increases in warmer conditions on the Chukchi shelf, resulting in larger age-0 individuals in fall (Bouchard et al., 2017), which are subsequently advected farther north. Under low to typical transport conditions, the age-0 Arctic cod, likely originating in the southern Chukchi or northern Bering Seas, have yet to be advected out of the southern and central shelf by late summer.

Under a third, “warming and increased transport” regime exemplified by 2019, when both northward transport and temperatures increased (Fig. 8c; Woodgate, 2018). Pelagic age-0 pollock and Arctic cod continue to be present on the Chukchi shelf in summer. As a result of increased transport, the residence time of age-0 gadids on the Chukchi shelf decreases. Under this regime, age-0 Arctic cod likely originate farther north than pollock; a nearly absent cold pool leads to a northward shift of the Arctic cod spawning population while adult pollock increasingly overwinter and spawn in the ice-free central and northern Bering Sea (Eisner et al., 2020) and possibly the southern Chukchi Sea (Emelin et al., 2022). Due to the increased northward transport, the
population of age-0 Arctic cod is displaced towards the Chukchi shelf break and Beaufort Sea by late summer. The consequences of this displacement are unknown for Arctic cod. For example, it may result in a potential timing mismatch of their ontogenetic migration to take advantage of warmer Atlantic water along the Chukchi and Beaufort shelf breaks during transport off the Chukchi shelf in fall (Geoffroy et al., 2016). Age-0 pollock that originate farther south in the northern Bering Sea would be transported into the Chukchi along with the warmer water masses and dominate the gadid distribution on the central and southern shelf in late summer.

Our analysis suggests that the anticipated continued warming of the Chukchi shelf (Danielson et al., 2020) will substantially alter ecosystem function. Under the two hypothetical environmental regimes representing the 2017 and 2019 surveys, the transition in gadid community structure could reduce the availability of high-quality prey to higher trophic levels in the Chukchi Sea as lower energy content subarctic species such as pollock continue to displace age-0 Arctic cod (Copeman et al., 2017).

Additionally, it remains unclear if these boreal species can establish permanent populations, given the persistent near-freezing temperatures they would later experience on the shelf in winter (Woodgate et al., 2005; Stabeno et al., 2018). Even if pollock do colonize the area as they have in the northern Bering Sea (Eisner et al. 2020), they may experience lower rates of overwinter survival than the endemic species and the size of the adult population will likely continue to depend on the migration of pollock into the area (Emelin et al., 2022). Arctic cod, which may experience reduced lipid storage as a result of higher metabolic demands or reduced food quality in warmer conditions (Copeman et al., 2022a), are at a higher risk of starvation as they transition
into wintering areas. A potential implication of this reduced survival would be a decrease in the total abundance of fishes in the Chukchi sea, at least on a seasonal basis.

Further work to identify the winter spawning locations of both the Arctic cod and pollock observed on the Chukchi shelf is needed to better constrain the relationship between spawning location and transport. Spawning grounds for Arctic cod in particular are difficult to confirm due to seasonal ice cover. Without direct observations and tracking of spawning populations, we have a limited understanding of the spatio-temporal distribution patterns exhibited by age-0 gadids as they develop and return as adults, and the key environmental drivers that determine juvenile and adult survival and reproductive success. Year-round in situ observations of Arctic cod migration and transport, for example through remote sampling of environmental DNA (Wietz et al., 2021) or target tracking from moored echosounders (Kaartvedt et al., 2009), are needed to further confirm and quantify the roles of transport in the distribution and movement of these fish.

If, as we hypothesize, the ongoing changes observed in the physical oceanography of the Chukchi Sea influence growth and transport of age-0 gadids, indirect environmental measurements could provide a basis for predicting future summer-time distributions of pelagic fishes in this region. Mooring-, satellite-, and shore-based observations as well as model-based predictions of ice, temperature, and transport are well established in the region (Frey et al., 2015; Woodgate, 2018; Janzen et al., 2019; Wang et al., 2018). These data sources are the basis for predictions of continued warming and higher transport into the Chukchi Sea. Northward shifts in the distribution of other marine animals have been associated with these changes in the
physical environment. For example, changes in water mass transport have strongly
influenced shifts in zooplankton distributions (Spear et al., 2020) which, in turn, have
influenced distribution shifts of their mobile predators (e.g. seabirds, Kuletz et al., 2020).
These shifts in populations, which are now also documented in the pelagic fish
community, provide insight into potential future states of the Chukchi ecosystem.
Developing a mechanistic understanding of how the anticipated rapid increases in
warming and transport in the Pacific Arctic will affect fishes is key to understanding
future impacts on pelagic fish communities, their role in the ecosystem, and effective
ecosystem management.

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Data Availability

All acoustic and biological datasets presented in this article are publicly available in DataONE (https://www.dataone.org): trawl data (2017: https://doi.org/10.24431/rw1k59h, 2019: https://doi.org/10.24431/rw1k59j), acoustic data (2017: https://doi.org/10.24431/rw1k59l, 2019: https://doi.org/10.24431/rw1k59k), and acoustic-trawl abundance estimates (2017: https://doi.org/10.24431/rw1k5b1, 2019: https://doi.org/10.24431/rw1k5b2).
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Table 1. Mean fish backscatter and total number of fish for abundant pelagic sound-scattering species, estimated with acoustic-trawl methods in 2017 and 2019. The total area of the survey region was $1.48 \times 10^5$ km$^2$ in 2017 and $1.53 \times 10^5$ km$^2$ in 2019, with $\sim92\%$ of the survey area overlapping between both years. Low abundance fishes, e.g. Pacific cod, make up a low proportion of the backscatter and thus their abundance estimates are more uncertain. However, these estimates are included here to provide a baseline for future assessments in the region.

<table>
<thead>
<tr>
<th>Species</th>
<th>2017</th>
<th>2019</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean fish backscatter ($s_A$, m$^2$ nmi$^{-2}$)</td>
<td>1094.8</td>
<td>239.6</td>
</tr>
<tr>
<td>Arctic cod</td>
<td>$5.6 \times 10^{11}$</td>
<td>$9.8 \times 10^{10}$</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>$1.5 \times 10^{11}$</td>
<td>$3.8 \times 10^{10}$</td>
</tr>
<tr>
<td>Capelin</td>
<td>$1.3 \times 10^{10}$</td>
<td>$2.3 \times 10^{9}$</td>
</tr>
<tr>
<td>Saffron cod</td>
<td>$1.5 \times 10^{9}$</td>
<td>$1.2 \times 10^{9}$</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>$2.7 \times 10^{9}$</td>
<td>$9.3 \times 10^{8}$</td>
</tr>
<tr>
<td>Pacific herring</td>
<td>Not present</td>
<td>$2.0 \times 10^{9}$</td>
</tr>
</tbody>
</table>
Fig. 1. Study area (highlighted by the red square on the inset map) in (a) 2017 and (b) 2019. The 40-, 100-, and 1000-m depth contours are shown.
**Fig. 2.** Catch composition as proportion of individuals captured in each midwater trawl in (a) 2017 and (b) 2019. 38 kHz backscatter from fishes ($s_A$, $m^2$ nmi$^{-2}$) along the survey transects during the c) 2017 and d) 2019 surveys. The size and color of each circle is proportional to the backscatter within each 0.5 nmi along-transect interval. The 40-, 100-, and 1000-m depth contours are shown.
Fig. 3. Density of Arctic cod estimated by acoustic-trawl methods in 0.5 nmi along-transect intervals in (a) 2012, (b) 2013, (c) 2017, and (d) 2019. Density of walleye pollock in (e) 2012, (f) 2013, (g) 2017, and (h) 2019. The 40-, 100-, and 1000-m depth contours are shown. In 2017 and 2019, the entire survey extent is shown. In 2012 and 2013, plots for Arctic cod (a, b) show only the region north of the Bering Strait (66 °N). This encompasses all Arctic cod except for an aggregation of large (age 1+) individuals captured in one trawl in 2012 at 65 N (not shown; see De Robertis et al. [2017b], their Fig. 2). (i) Mean areal density (fish m$^{-2}$) of Arctic cod and pollock north of 66 °N. Pollock were present in 2012, but their density was too low to be visible.
Fig. 4. Size distributions estimated by acoustic-trawl methods of (a) Arctic cod and (b) walleye pollock in each survey year.
**Fig. 5.** Surface and bottom temperature and salinity at CTD stations in (a, b) 2012, (c, d) 2013, (e, f) 2017, and (g, h) 2019, where the size of each point indicates the abundance of Arctic cod (green) and walleye pollock (purple) in the transect intervals associated with the station (see methods for details). CTD stations where fish density in the associated transect intervals was < 0.001 fish m$^{-2}$ are indicated by a black x.
**Fig. 6.** Total abundance of Arctic cod (green) and walleye pollock (purple) by depth in the water column in (a, b) 2017 and (c, d) 2019. The lines in each panel partition the total abundance into regions where bottom temperatures were >2 °C (orange) and <2 °C (blue).
Fig. 7. Mean transport (black dashed line) and bottom temperatures (blue dotted line) measured at Bering Strait (A3 mooring, Woodgate, 2018; Woodgate and Peralta-Ferriz, 2021) from January to August of each year (1998 - 2019). The years of the acoustic-trawl surveys (2012, 2013, 2017, 2019) are indicated by the grey-shaded regions.
Fig. 8. Hypothesized climate-driven shifts in the late summer distribution of the dominant pelagic gadids in the Chukchi Sea. (a) Under recent conditions of later ice retreat (2012 and 2013), Arctic cod are present in intermediate and cool waters across the Chukchi Shelf. (b) With increased warming and early ice retreat (2017), age-0 Arctic cod increase in abundance and size as a result of increasing temperatures. Increased presence of adult walleye pollock in the northern Bering Sea results in the transport of age-0 pollock into the Chukchi, where conditions are favorable for both gadid species. (c) With increased transport of warmer waters from the Bering Sea (2019), Arctic cod are displaced farther north, along with the intermediate temperature waters. Age-0 pollock from the northern Bering Sea are transported with the warmer waters and become the dominant gadid in the southern portion of the shelf. The 1000-m depth contour is shown to indicate the Chukchi shelf break.
### Supplementary Figures and Tables

**Table A.1.** Linear models used to convert total length (TL) to standard length (SL), total length to fork length (FL), and standard length to fork length based on the different length measurements taken on the same fish specimen. Number of observations (n) and the range of lengths used to fit each model are included. All models were statistically significant (p<0.001).

<table>
<thead>
<tr>
<th>Species</th>
<th>X</th>
<th>Y</th>
<th>n</th>
<th>Length range in model (mm)</th>
<th>Intercept</th>
<th>Slope</th>
<th>R²</th>
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<td>Arctic cod</td>
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<td>SL</td>
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<td>28-230</td>
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Fig. A.1. Timing of transect sampling in the Chukchi Sea in (a) 2012, (b) 2013, (c) 2017, and (d) 2019. The color of the transect indicates the yearday of the survey trackline. In 2017, a nearshore portion of the survey area was sampled from 11-17 August in agreement with the coastal communities to vacate the area prior to subsistence harvest activities.
Fig. A.2. Daily mean length of Arctic cod as a function of yearday in the four years of acoustic-trawl surveys. The size of each circle is scaled to mean density of Arctic cod (fish m\(^{-2}\)) observed on each day, normalized to the mean density observed in each survey.
Fig. A.3. Density (fish m$^{-2}$) of (a, e) capelin, (b, f) saffron cod, (c, g) Pacific cod, and (d, h) Pacific herring estimated by acoustic-trawl methods in 0.5 nmi along-track intervals in 2017 (top row) and 2019 (bottom row). The 40-, 100-, and 1000-m depth contours are shown.
Fig. A.4. Linearly interpolated mean surface (top row) and bottom (bottom row, see methods for details) temperatures observed in CTD profiles in (a, e) 2012, (b, f) 2013, (c, g) 2017, and (d, h) 2019. Hatching indicates regions where bottom temperatures were <2 °C.
Fig. A.5. Mean winter (January, February, March), spring (April, May, June) and summer (July, August, September) a) bottom temperature and b) transport observed at Bering Strait A3 mooring (Woodgate, 2018; Woodgate and Peralta-Ferriz, 2021). The years of the acoustic-trawl surveys (2012, 2013, 2017, 2019) are indicated by the grey-shaded regions.

Fig. A.5 References


Species identifications made during field sampling were modified based on the genetic verification of species identity described in Wildes et al. (2022). In the midwater trawls, 40% of all gadid specimens ($n = 2244$) in 2017 and 56% of all fish specimens in 2019 ($n = 5676$) were genetically confirmed. Unverified specimens <24 cm in length were assigned to a species as a function of the gadid species proportion-at-length in each trawl as described below. In practice, only 59 specimens >10 cm in length were modified as a result of the model reassignment, which constitutes 0.3 % of all measured specimens. All fish >= 24 cm retained their species identification as determined in the field.

For a given trawl, the proportions of each of the five gadid species ($B. saida$, $G. chalcogrammus$, $E. gracilis$, $G. macrocephalus$, and $A. glacialis$) were determined from the genetically confirmed specimens. Proportions of each species were calculated for specimen grouped into the following length classes: 2 cm <= standard length (SL) < 4 cm, 4 <= SL < 6 cm, and 6 cm <= SL < 30 cm. The proportion ($P$) of a species $s$ of length class $l$ in trawl $t$ was calculated from the number of genetically confirmed individuals ($N$) of species $s$ of length class $l$ from trawl $t$,

$$P_{s,t,l} = \frac{N_{s,t,l}}{\sum_{s} N_{s,t,l}}$$

For each specimen that was not genetically analyzed, a species was assigned based on the determined genetically identified proportions. For example, trawl $t$ contains the
following probabilities $P$ for length class $l$: $P_{s_1,t,l} = 0.55$, $P_{s_2,t,l} = 0.25$, $P_{s_3,t,l} = 0.2$, $P_{s_4,t,l} = 0$, and $P_{s_5,t,l} = 0$. A value $x$ is randomly generated where $0 < x \leq 1$. The specimen is assigned to species $s$ based on the following conditions:

$$s = \begin{cases} 
  s_1, & x \leq P_{s_1,t,l} \\
  s_2, & P_{s_1,t,l} < x \leq P_{s_1,t,l} + P_{s_2,t,l} \\
  \ldots \\
  s_n, & P_{s_1,t,l} + P_{s_2,t,l} + \ldots + P_{s_{n-1},t,l} < x \leq P_{s_1,t,l} + P_{s_2,t,l} + \ldots + P_{s_n,t,l}
\end{cases}$$

To evaluate the performance of the genetic reassignment model, the identity of all genetically identified specimens were predicted using a leave-one-out method. The identity of each individual was predicted based on the other genetically identified gadid specimens from the same trawl haul. The model-predicted species matched the genetic identification for >80% for individuals in both years. The allocation of acoustic backscatter from trawl data is based on the length distribution and the proportion of each species in the catch, thus the model was also evaluated based on the ability to predict the proportions of each gadid species in each trawl and the impact of reassignment on the length distributions of each species.

The model reassignment introduces a random element due to the probabilistic species assignment of the specimens which were not genetically identified. However, the average species compositions of gadids in a given haul after reassignment exhibited very little difference to those derived from the genetically identified specimens (Fig. B.1). The mean of the absolute difference between the proportions of Arctic cod and pollock from only genetic specimens and all specimens for each haul was <5% in 2017 and <3% in 2019. The higher variability in 2017 is likely due to both a greater spatial overlap between species, and greater overlap.
in their size composition (Fig. B.2) and a higher proportion of unconfirmed identifications than in 2019.

To quantify agreements in length between genetically identified versus all specimens, we calculated the two-sample Kolmogorov-Smirnov (KS) test between the known and model-assigned lengths for each gadid species in each trawl. The KS statistic was not significant in any trawls, indicating no significant differences between the length-frequency distributions between the genetically confirmed specimens and all specimens after model reassignment. Mean absolute differences between known and reassigned mean species length in each trawl haul were < 0.5 cm for both Arctic cod and pollock in both years (pollock: 0.43 in 2017 and 0.23 in 2019, Arctic cod: 0.07 in 2017 and 0.09 in 2019).

When catches were subsampled, total catch weights and abundances were modified based on the updated identifications of specimens to accurately reflect the final species composition in each trawl catch. This can introduce changes in the weight and number of individuals of a given species in a trawl haul due to the extrapolation from the measured subsamples to the total catch (Figs. B.3, B.4). To evaluate the potential changes to the total catch resulting from species reassignments, total weight, total number, sampled weight, and sampled number of each gadid species in each trawl in both years were calculated from the original field assignments and the genetically reassigned data. Changes to these measures as a result of reassignment were typically <0.5% (sum of the total number of gadid species present in each trawl in each year; n = 106 in 2017, n = 92 in 2019), with only 5 samples across both years showing changes in any of the metrics by >1% (Figs. B.3 and B.4). These errors were identified as a result
of rounding errors for the mean weight of individuals (i.e. mean individual weights were
assigned as 0.002 kg rather than 0.001 kg) introduced by the 0.001 kg precision used in
the field collection database.
Fig. B.1. Comparison of the proportion of (a, c) Arctic cod and (b, d) walleye pollock in each trawl determined from only the genetically confirmed specimens, and from all specimens after model reassignment. Mean absolute difference between the proportions from only genetic specimens and all specimens for each haul is indicated for each set of measurements.
Fig. B.2. Proportion at length of genetically identified Arctic cod and pollock in (a) 2017 and (b) 2019.
Fig. B.3. Comparison of field and reassigned (a) total weight, (b) total number, (c) sampled weight, and (d) sampled number of gadids for all 2017 trawls. Each point represents the total for a single gadid species in a trawl. Mean and maximum values of the absolute difference between the field and reassigned values for each haul are indicated for each set of measurements.
Fig. B.4. Comparison of field and reassigned (a) total weight, (b) total number, (c) sampled weight, and (c) sampled number of gadids 2019 for all trawls. Each point represents the total for a single gadid species in a trawl. Mean and maximum values of the absolute difference between the field and reassigned values for each haul are indicated for each set of measurements.